

Environmental factors shaping ungulate abundances in Poland

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Abstract Population densities of large herbivores are determined by the diverse effects of density-dependent and independent environmental factors. In this study, we used the official 1998–2003 inventory data on ungulate numbers from 462 forest districts and 23 national parks across Poland to determine the roles of various environmental factors in shaping country-wide spatial patterns of ungulate abundances. Spatially explicit generalized additive mixed models showed that different sets of environmental variables explained 39 to 50 % of the variation in red deer *Cervus elaphus*, wild boar *Sus scrofa*, and roe deer *Capreolus capreolus* abundances. For all of the studied species, low forest cover and the mean January temperature were the most important factors limiting their numbers. Woodland cover above 40–50 % held the highest densities for these species. Wild boar and roe deer were more numerous in deciduous or mixed woodlands within a matrix of arable land. Furthermore, we found significant positive effects of marshes and water bodies on wild boar abundances. A juxtaposition of obtained results with ongoing environmental changes (global warming, increase in forest cover) may indicate future growth in ungulate distributions and numbers.

Keywords Forest cover · January temperature · Arable land · Red deer · Roe deer · Wild boar

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Introduction

Ungulate population dynamics are shaped by density-dependent and independent factors (Saether 1997; Jędrzejewska and Jędrzejewski 2005; Brown 2011). These influence the population vital rates, which often leads to changes in population numbers (Jorgenson et al. 1993; Willisch et al. 2013). In temperate environments and at high population densities, intraspecific competition for food increases winter mortality and reduces fecundity rate (Clutton-Brock et al. 1987a; Capurro et al. 1997; Coulson et al. 2000). Furthermore, population density influences the age of maturity and pregnancy rate among females (Clutton-Brock et al. 1985, 1987b). Among density-independent factors, weather conditions have significant and multidirectional effects on ungulate demography, operating mainly through changes in mortality or indirectly through the quantity and quality of food (Post and Stenseth 1999; Hone and Clutton-Brock 2007). For example, harsh winter conditions affected the survival rate of Soay sheep (Milner et al. 1999; Coulson et al. 2001), red deer (*Cervus elaphus*; Forchhammer et al. 1998), and roe deer (*Capreolus capreolus*; Gaillard et al. 1993), and they shaped recruitment in mountain-dwelling woodland caribou (*Rangifer tarandus caribou*; Hegel et al. 2010). Autumn weather influenced reproduction rates of female white-tailed deer (*Odocoileus virginianus*), while spring weather conditions affected their reproductive success (Simard et al. 2010). In red deer, the weight at birth was influenced by rainfall in winter and temperature in spring (Sims et al. 2007). The annual variations in weather influenced the time and rate of plant green-up which affected the juvenile growth of bighorn sheep (*Ovis canadensis*) and mountain goat (*Oreamnos americanus*), the survival of bighorn sheep and Alpine ibex (*Capra ibex*; Pettorelli et al. 2007), and the age of first reproduction in red deer (Langvatn et al. 1996).

Ungulates in many regions are subjected to hunting and predation. The effects of predation on ungulate density have

been a controversial issue. Several studies confirm a density-dependent regulatory role of predation (Ballard and Miller 1990; Messier 1994), and others show predation as a density-independent limiting factor (Larsen et al. 1989; Boutin 1992; Jędrzejewska et al. 1997). Interestingly, predators appear to have diverse effects on different ungulate species (higher for small-sized ungulates) or the same species at different density levels (Hayes et al. 2003; Jędrzejewska and Jędrzejewski 2005).

Whereas most of the above-mentioned studies explored the effects of density-dependent and independent factors on ungulate population at a local scale, broad-scale country-wide analyses of factors shaping variation in ungulate density are rare. Our study aims to fill this gap. Based on official data on numbers of three of the most abundant ungulates in Poland (red deer, roe deer, and wild boar (*Sus scrofa*)), we (1) evaluate which environmental factors correlate with spatial variation in ungulate densities, (2) determine the significance of the relationships between explanatory variables and ungulate abundances, and (3) discuss the applicability of the obtained results in predicting future demographic and distribution trends for ungulates.

Study area

Annual game censuses cover the whole of Poland (311,904 km², 49°00'–54°50' N, 14°08'–24°09' E). Poland is a largely lowland country with plains (<300 m a.s.l.) constituting 91 % of the area. Uplands (301–500 m a.s.l.) cover 6 % and mountains (500–2,499 m a.s.l.) 3 % of the country. Geographical regions change with latitude: from lowlands in northern and central Poland to uplands and mountains in the south. Poland is located in the temperate climate zone with a transitional character (Atlantic influences in the west and continental in the east). The mean annual temperatures are highest in south-western and south-eastern Poland (8.5 °C) and lowest in the north-east (6 °C). The mean January temperature varies from –8 °C in the mountains to –1 °C in the western part of the country. The mean temperature of July ranges from 10 °C in the mountains to 16.5 °C at the Baltic Sea coast and 19 °C in the south west. Annual precipitation is 500–650 mm in the lowlands and 1,200–1,500 mm in the mountains (Central Statistical Office 2011a).

Nearly 99 % of Poland lies in the Baltic Basin (including 56 % in the Vistula River Basin and 34 % in the Odra River Basin). Almost 1 % of the country is covered by lakes >0.01 km² ($n=9,300$). The majority are glacial lakes occurring in the Masurian and Pomerania Lakelands in the north of the country.

The mean human population density is 122 inhabitants/km² and varies from 20 in north-western and north-eastern Poland to

500 inhabitants/km² in Upper Silesia, SW Poland (Central Statistical Office 2011b). The mean density of roads (motorways) was 80.7 km/100 km² in 2004. Around 60 % of Poland's area is covered by farmlands with a predominance of arable lands (90 % of farmlands) and smaller shares of meadows and orchards.

Forests cover 29 % of the country (Fig. 1). The majority of forests are coniferous stands dominated by Scots pine (*Pinus sylvestris*, 60 % of forest area) and Norway spruce (*Picea abies*, 6 %). Deciduous and mixed forest consisting of oak (*Quercus robur* and *Quercus petraea*), ash (*Fraxinus excelsior*), maple (*Acer platanoides* and *Acer pseudoplatanus*), beech (*Fagus sylvatica*), hornbeam (*Carpinus betulus*), birch (*Betula verrucosa* and *Betula pubescens*), and alder (*Alnus glutinosa*) constitute about 25 % of all forest land (Central Statistical Office 2011c). About 98 % of woodlands are commercial stands and only 2 % are national parks and reserves. Most of the commercial stands are State Forests (83 %), the rest remain private property. The State Forests are divided into 439 forest districts (in 2003). Their size varies from 89 to 2,501 km² ($\bar{x}=701$ km², $SD=417.8$ km²) depending on forest cover (forest district size is inversely proportional to the amount of forest cover). Among 23 national parks, Biebrza National Park (NP) is the largest (592 km²), whereas Ojców NP is the smallest (22 km²) ($\bar{x}=136.8$ km², $SD=132.6$ km²; Central Statistical Office 2011c).

Three native species of ungulates occur throughout Poland: red deer, wild boar, and roe deer. In the north-eastern and eastern parts of the country, moose (*Alces alces*) and a few isolated populations of European bison (*Bison bonasus*) also occur. An endangered population of chamois (*Rupicapra rupicapra*) persists in the Tatra Mountains

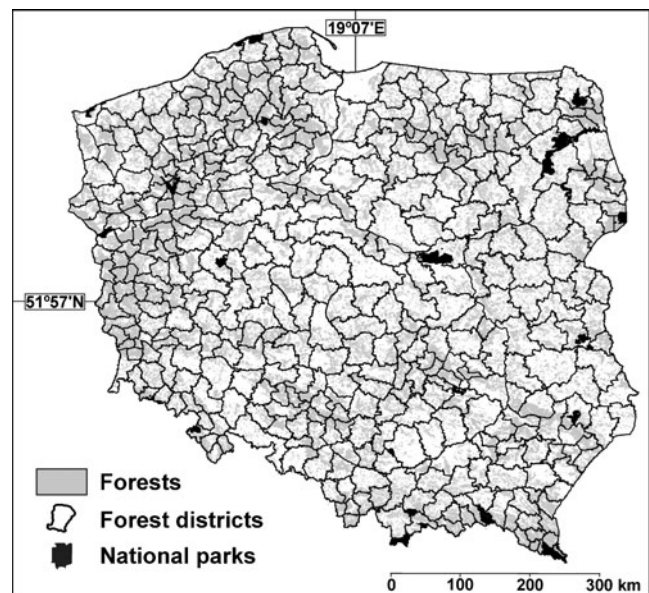


Fig. 1 Distribution of sample areas (forest districts, national parks) and forests in Poland during 1999–2003

(Wawrzyniak et al. 2010). Red deer, wild boar, roe deer, and moose are game species. In order to increase moose numbers in Poland, a ban on hunting this species was introduced in 2001. Hunting seasons for other species generally cover autumn and early winter. The exceptions are red deer males which are hunted before and during the rutting season in late summer and autumn, roe deer males can be harvested in late spring and summer (including the rut), and wild boar males and juveniles that are shot in all months except March (Wawrzyniak et al. 2010). European bison and chamois are protected species. In the past, three alien species of ungulates were introduced to the forests of western Poland: fallow deer (*Dama dama*), sika deer (*Cervus nippon*), and mouflon (*Ovis musimon*). Currently, these are game species hunted in autumn and winter. North-eastern, eastern, and south-eastern regions are inhabited by viable populations of large predators such as the wolf (*Canis lupus*) and lynx (*Lynx lynx*) (Niedziałkowska et al. 2006; Jędrzejewski et al. 2008). The Carpathians harbor a population of brown bear (*Ursus arctos*).

Material and methods

Data collection

Official data on ungulate numbers were obtained from all State Forest districts ($n=439$) and national parks ($n=23$) during 1998–2003. Every year during this period, members of hunting clubs and staff of forest districts and national parks attempted to estimate ungulate numbers (red deer, roe deer, and wild boar) in managed areas. Two census methods were used. The most common were year-round observations. Every year at the beginning of spring (end of March), hunters and foresters, based on their field observations and subjective expert opinions, assessed population numbers of ungulates in hunting grounds (from 1 to 27 hunting grounds for each forest district; hunting ground area—range 15–157 km²). National park rangers carried out the same assessment in national parks (area—range 22–605 km²). Three forest districts performed drive censuses. Forest compartments to be counted using this method were randomly selected (covering about 10 % of surveyed areas). During the drive census, each chosen forest compartment or block of adjoining compartments was surrounded by observers, who stationed themselves at intervals of 50–100 m to maintain visual contact. The observers along three sides remained stationary, while those along the fourth side moved inward and went through the entire area. The observers (both stationary and moving) noted ungulates passing through the line of observers (on their right hand side only) and whether the ungulates were entering or leaving the closed area being censused (Pucek et al. 1975; Jędrzejewska

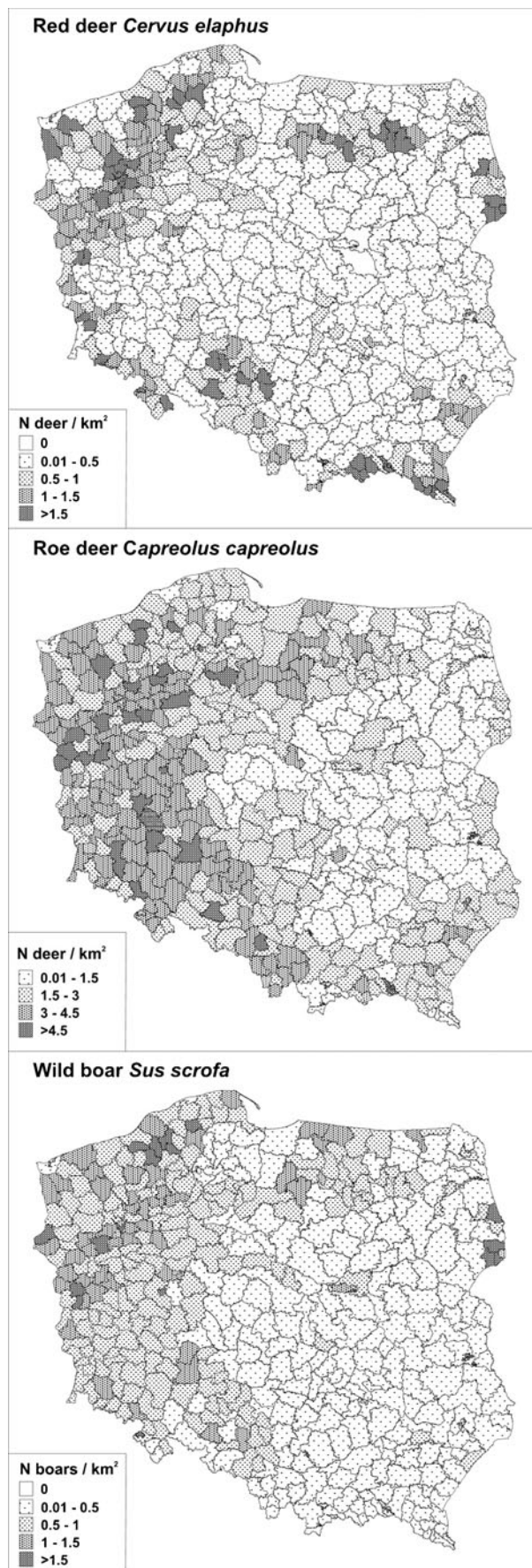
et al. 1997; Borkowski et al. 2011). Collected observations were summed and served as estimates.

Data analyses

We computed abundance indices (number per square kilometer) for red deer, roe deer, and wild boar by dividing their official numbers (averaged over 5 years for each forest district and national park, $N=462$) by the area of inventory unit (forest district or national park; $\bar{x}=673.2$ km², $SD=426.3$ km², range 22–2,501 km²; Fig. 2). For each inventory unit, we also calculated the following parameters: (1) percentage of forest cover, (2) deciduous and mixed forests as a proportion of forest that is either broad-leaved or mixed, (3) arable land (proportion of nonforested land that is arable), (4) marshes (proportion of nonforested land that is marsh), (5) pastures (proportion of nonforested land that is pasture), and (6) proportion of open water. In addition, we measured the length of (7) main roads (international and national motorways), (8) secondary (regional) roads, (9) railways, and estimated (10) the number of villages (usually <1,000 inhabitants), (11) human population density, and (12) the mean January temperature. The variables from 1 to 6 were obtained from the Corine Land Cover 2000 database available on the website of the Institute of Geodesy and Cartography [IGC] (2011) (www.igik.edu.pl). Variables 7–10 were measured on digital maps prepared by the IMAGIS Company. The human population density for the year 2002 (11) was determined using data available on the website of the Institute of Geography and Spatial Organization [IGSO], Polish Academy of Science (2011) (www.igipz.pan.pl/). January temperatures (12) were obtained from the Agroclimate model described at the Institute of Soil Science and Plant Cultivation, State Research Institute, Department of Agrometeorology and Applied Informatics [DAAI] (2011) (www.zazi.iung.pulawy.pl) for a subset of only 129 units distributed regularly across Poland. We applied interpolation to the remaining 333 units using a generalized additive model (GAM) with a bivariate nonlinear term of the latitude and longitude (Wood 2006). There was no spatial autocorrelation detectable in the residuals of the GAM, indicating that the spatial trend was adequately captured. For the analyses, we used the observed values of January temperatures where available and the GAM predictions elsewhere.

We examined collinearity between the potential explanatory variables by calculating pairwise correlation coefficients. Due to high correlations between predictor covariates ($R^2>0.4$) only those judged to be most relevant and uncorrelated were considered as candidates for inclusion in the models: forest cover, deciduous and mixed forest, arable land, marsh, water, and the mean January temperature.

We were not able to include large predator (wolf and lynx) effects (expressed as predator density) and official



◀ **Fig. 2** Abundance indices of red deer, roe deer, and wild boar in forest districts ($n=439$) and national parks (23) in Poland during 1999–2003

data on hunting bags in our final models. Predator effects were highly correlated with forest cover (the most informative explanatory variable). Hunting bags were estimated as a proportion of spring estimates (Wawrzyniak et al. 2010) used as dependent variable in our models.

As the response variables (red deer, roe deer, and wild boar abundance indices) presented strong right skewness of the value distribution, we applied log-transformation before modeling (Sokal and Rohlf 1995). In order to determine factors effecting ungulate abundances, we used generalized additive mixed models (GAMMs) relating the abundances of the species to environmental covariates (Wood 2006). Smooth terms of the covariates were used to allow for nonlinear responses to the covariates, and spatial autocorrelation was accounted for by including a spherical correlation structure in the model (Pinheiro and Bates 2000). Given the potentially high dimensionality of the models, we opted for a forward selection procedure. Covariates were included sequentially, starting with those showing the highest correlation coefficient with the response variable. When a covariate showed evidence for a nonlinear relationship to the species abundance in an exploratory analysis with locally weighted polynomial regression (estimated degrees of freedom [edf]>1), we included it as a nonlinear term in the models using spline functions to test for nonlinearity. Covariates were retained in the model when the associated coefficient was significantly different from zero.

Results

Red deer occur throughout Poland except for two forest districts located around Warsaw, central Poland (Fig. 2). The highest indices of red deer abundance were found in the montane regions of southern Poland and in the large woodlands in western and north-eastern parts of the country. The predictor variables selected in the GAMM for red deer abundance indices were forest cover, the mean January temperature, and arable land (Table 1). The range of the spatial correlation (the distance beyond which data values were no longer spatially autocorrelated) was estimated at 1.49° (about 165 km). The proportion of variance explained by the final model equaled 50 %. Forest cover and the mean January temperature had a similar effect on deer abundance indices ($P<0.001$), with arable land having a weaker impact ($P=0.008$). The final model indicated a positive linear relationship between red deer abundance indices and the mean January temperature and a negative relationship with arable land (Fig. 3). Nonlinear relationship between species

Table 1 Effects of environmental factors on red deer, roe deer, and wild boar abundance indices in Poland: results of generalized additive mixed models (GAMMs). The models include a spherical spatial correlation function for the residuals with parameters: range (the

distance at which residuals are no longer autocorrelated, in decimal degrees, and in kilometers) and the nugget (correlation at distance zero). Environmental factors: forest cover, January temperature, arable land, deciduous and mixed forest, marsh, and water

Model	Linear terms				Nonlinear terms			R_{adj}^2	Range	Nugget
Parameter	Coefficient	SE	<i>t</i>	<i>P</i>	edf	<i>F</i>	<i>P</i>			
Red deer										
Intercept	−0.41	0.28	−1.49	0.137				0.50	1.49° (165 km)	0.16
Forest cover					4.51	105.44	<0.001			
January temperature	0.27	0.06	4.68	<0.001						
Arable land	−0.51	0.18	−2.78	0.006						
Roe deer										
Intercept	0.98	0.13	7.56	<0.001				0.39	1.60° (178 km)	0.59
January temperature	0.29	0.03	9.27	<0.001						
Forest cover					3.33	25.97	<0.001			
Deciduous and mixed forest	0.50	0.09	5.70	<0.001						
Arable land	0.34	0.11	3.42	<0.001						
Wild boar										
Intercept	−1.20	0.07	−16.25	<0.001				0.47	0.04° (4 km)	0.09
January temperature					4.59	53.11	<0.001			
Forest cover					3.14	25.67	<0.001			
Marsh	0.35	0.09	4.05	<0.001						
Deciduous and mixed forest	0.57	0.15	3.82	<0.001						
Water	0.16	0.04	3.55	<0.001						
Arable land					2.24	6.62	<0.001			

edf estimated degrees of freedom

abundance indices and forest cover showed a clear positive effect of this variable (edf=4.51, Fig. 3). Red deer abundance increased with a growing proportion of forest cover, with a slight inflection after 40 % (Fig. 3).

The range of roe deer covers the whole Poland, though in central and eastern regions this species is less abundant (Fig. 2). The most parsimonious GAMMs for roe deer comprised four explanatory variables: forest cover, the mean January temperature, deciduous and mixed forest, and arable land. Spatial autocorrelation range equaled 1.60° (about 178 km). Predictor covariates accounted for 39 % of the variation, with forest cover, the mean January temperature, and deciduous and mixed forest having the strongest impact ($P<0.001$, Table 1). The results indicated a nonlinear response of roe deer abundance to forest cover (edf=3.33). Increasing forest cover positively influenced roe deer abundance indices along the entire gradient of covariate values. However, the initial growth plateaued after reaching 50 % (Fig. 4). The other variables exhibited a positive linear relationship with the species abundance indices.

Wild boars inhabit the whole country, with the exception of the Tatra Mountains in the south (Fig. 2). This species was notably more common in western than in eastern Poland. The final GAMMs for wild boar included six

predictor covariates: the mean January temperature, forest cover, marsh, deciduous and mixed forest, water, and arable land. Spatial autocorrelation of predictor variables was detected only to the range of 0.04° (4 km). The fitted model explained 47 % of the variation. GAMM indicated a nonlinear relationship between the abundance indices and the mean January temperature (edf=4.59, $P<0.001$), forest cover (edf=3.14, $P<0.001$), and arable land (edf=2.24, $P<0.001$) and a positive linear relationship for marsh ($P<0.001$), deciduous and mixed forest ($P<0.001$), and water ($P<0.001$, Table 1). The positive influence of increasing mean January temperature on species abundance was most conspicuous at values above −3 °C. The change in the direction of the relationship (from positive to negative) at temperatures between −5 and 4 °C might result from sparse data points (high standard errors), which indicates uncertainty in the effect of the mean January temperature at lower values (Fig. 5). Increasing forest cover had a constant and positive effect on abundance indices, reaching a plateau at 40 %. Marsh influence, though highly significant, could have been diluted by a small amount of data points at proportions >10 % (high standard errors). The positive effect of arable land on wild boar abundance indices declined after attaining 40 % (Fig. 5).

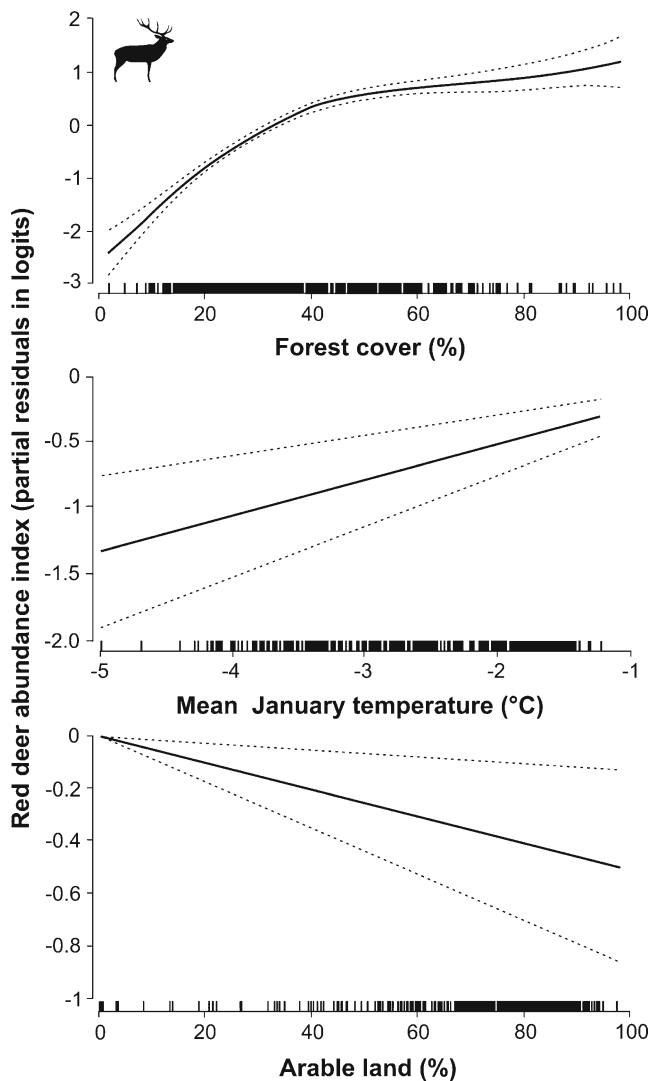


Fig. 3 Effects of environmental factors on red deer abundance indices in Poland: results of generalized additive mixed models (GAMMs). The distribution of explanatory variable values is marked with *black vertical lines* on the *x*-axis. The *y*-axis presents the partial residuals of the model after removing the effects of the other covariates. The slope of zero indicates a constant influence of the covariates on red deer abundance indices. *Dashed lines* correspond to 1 SE. Environmental factors: forest cover, January temperature, arable land, deciduous and mixed forest, marsh, and water

Discussion

As evidenced for various ungulate species (Coulson et al. 2001; Simard et al. 2010), environmental factors have a considerable influence on ungulate abundances also in Poland. Red deer numbers were strongly influenced by forest cover, which explains the high abundance of this species in southern, western, and north-eastern Poland, where large woodlands occur and forest cover often exceeds 40 % (Central Statistical Office 2004). Currently, forest is considered to be an optimal habitat type for red deer in Europe, as it provides the species with various food

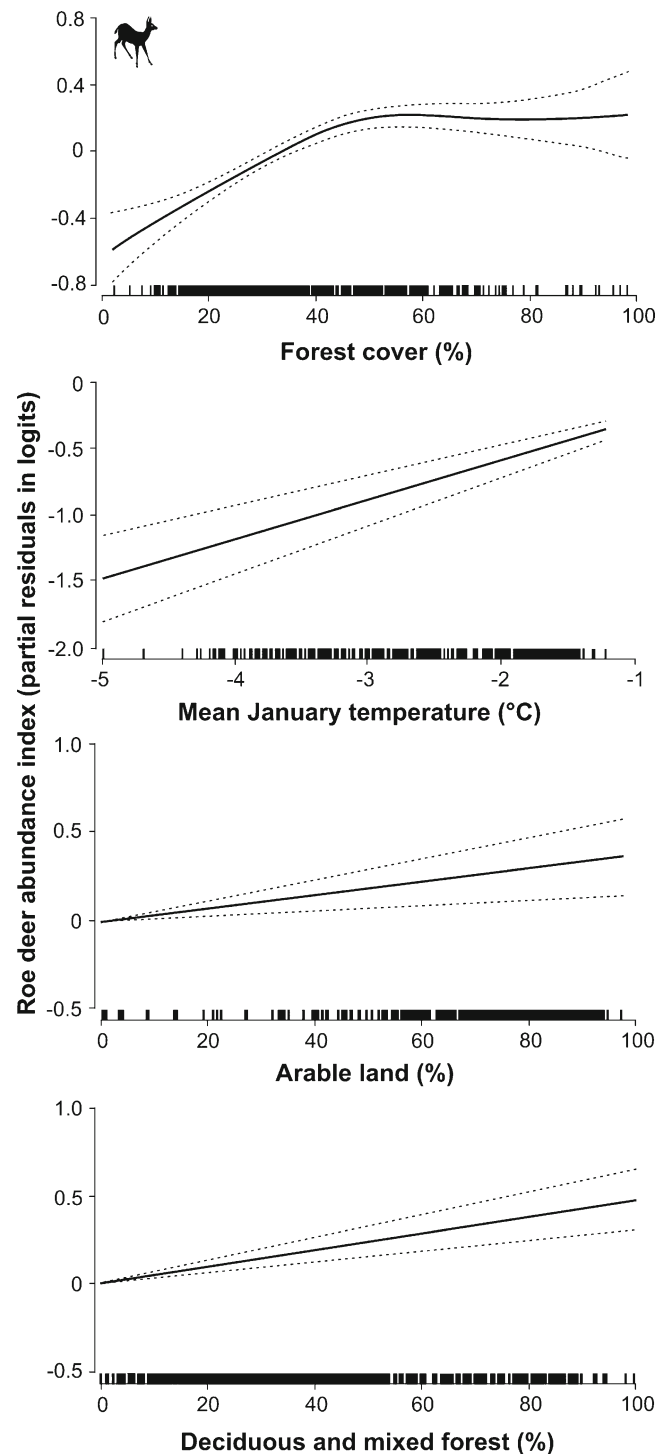


Fig. 4 Effects of environmental factors on roe deer abundance indices in Poland: results of generalized additive mixed models (GAMMs). The distribution of explanatory variable values is marked with *black vertical lines* on the *x*-axis. The *y*-axis presents the partial residuals of the model after removing the effects of the other covariates. The slope of zero indicates a constant influence of the covariates on roe deer abundance indices. *Dashed lines* correspond to 1 SE. Environmental factors: forest cover, January temperature, arable land, deciduous and mixed forest, marsh, and water

resources (herbs, grasses, twigs, barks, acorns) throughout the year (Dzięgielewski 1970). Although previous findings (Dzięciołowski 1991; Jędrzejewska et al. 1994) reported that some red deer populations in Poland prefer deciduous woodlands, we did not find this to be the case at the larger, national scale. The lack of marshes among explanatory variables in the final model, and the negative impact of increasing arable land proportions in open areas, confirmed the low relevance of these habitat types for red deer. As shown by Dzięciołowski (1991), the importance of fields for this species is limited to the spring–summer period when animals are occasionally leaving the forest and forage on crop fields. However, the observed increase in the number and geographic distribution of the species in Poland (Central Statistical Office 2004) may enhance the role of arable land as deer habitat. This situation was observed in the lowlands of Great Britain (Putman and Moore 1998).

Climatic conditions (temperature, precipitation, and snow depth) were found to influence the population demography and dynamics of ungulates by affecting plant productivity or, more directly, by forcing energetic demands or behavioral restraints (Saether 1997; Martinez-Jauregui et al. 2009). Loison and Langvatn (1998) analyzed red deer densities in Norway and found that deep snow and high wind speed were correlated with low red deer densities. In the case of Polish red deer populations, the mean January temperature negatively affected population dynamics directly through winter mortality (Okarma et al. 1995). Our study confirmed the positive influence of an increasing mean January temperature on red deer abundance. As temperatures in Poland exhibit a longitudinal gradient—decreasing from west to east with montane regions in the south being an exception (elevation temperature zones; Lorenc 2005)—the highest red deer numbers were recorded in units located in the western and north-western parts of the country.

The roe deer is regarded as the ungulate with the largest ecological plasticity (Cagnacci et al. 2011) and we therefore expected this species to be less affected by environmental factors. Our model indicated forest cover to be the most influential factor of roe deer abundance. Areas with forest cover above 50 % held the highest abundances of roe deer. The positive effect of increasing forest cover on roe deer abundance was also found by Melis et al. (2009) on a European scale. Roe deer, the species typically considered to be adapted to woodlands (Hewison et al. 1998), selects forests for cover (Mysterud and Ostbye 1999) and forage (Van Moorter et al. 2009). The species is a generalist, but also a highly selective herbivore that feeds on a variety of plant species (Duncan et al. 1998) and prefers forests rich in multispecies herb and bush layers (Barancekova 2004). Pucek et al. (1975) reported a higher density of roe deer in Polish deciduous and mixed forests, where most diverse ground vegetation occurs. The same positive influence of

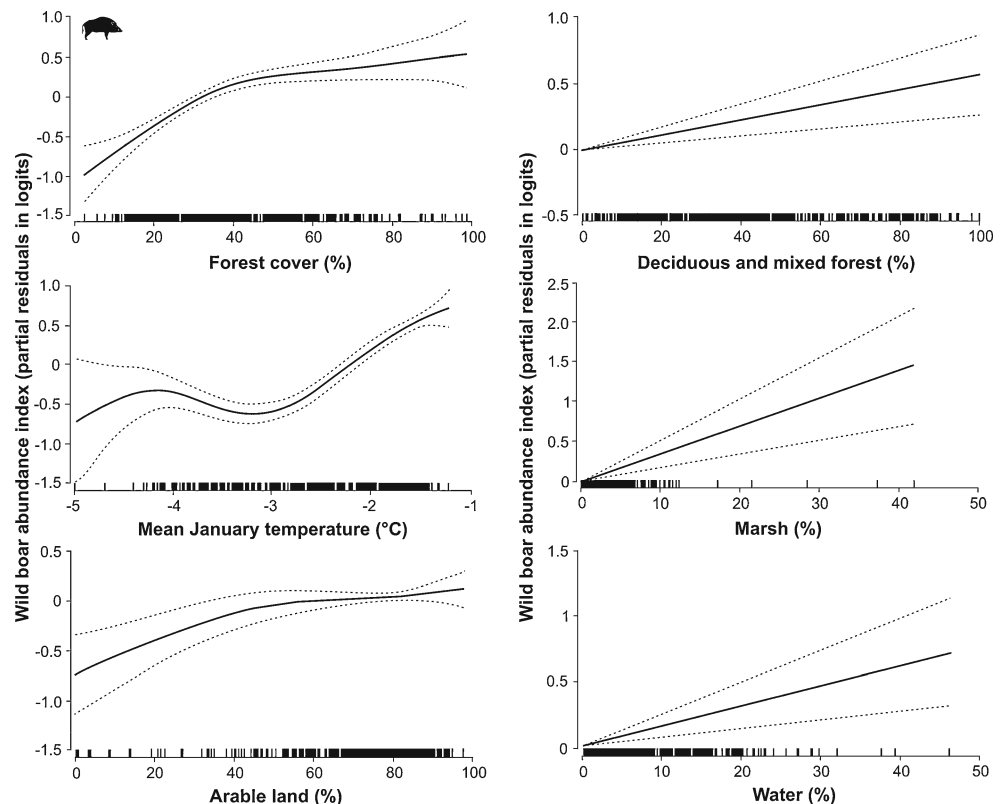
increasing proportion of deciduous and mixed forest stands was confirmed by our final model. In Great Britain, coniferous forests are favored by roe deer only when they provide high availability of clear-cuts and young plantations (Putman 1994).

The growth in proportion of arable land had a positive effect on roe deer numbers. Though roe deer predominantly inhabited forests in the past, they adapted to agricultural habitats following broad-scale deforestation (Hewison et al. 1998). Agricultural landscapes facilitate roe deer by providing high quality food (Hewison et al. 2009; Abbas et al. 2011). Hence, nowadays there are roe deer herds not depending on forest habitats (Fruziński et al. 1982; Hewison et al. 2001; Sönnichsen et al. 2013).

An increase in mean January temperature positively affected roe deer abundances. Holand et al. (1998) listed heavy foot loading, small body size, and low brisket height as factors challenging roe deer during adverse winter conditions. Okarma et al. (1995) in Poland and Kiili (1991) in Estonia found a relationship between severe winter weather and the number of adult mortalities from exhaustion, hunger, and predation. Similar to red deer, roe deer have the most favorable weather conditions in western Poland, where the species is most abundant.

Wild boar abundance indices were profoundly influenced by forest cover. Areas where forest cover exceeds 40 % had the highest abundances of the species. A similar relationship was confirmed by Virgos (2002) in Spain where wild boars occurred more frequently in areas comprising larger forest fragments. The positive influence of forest cover on wild boar abundance is primarily related to food supply and shelter (Massei et al. 1996; Schley and Roper 2003). Herrero et al. (2008) showed the multidirectional importance of shelter availability on the performance of two Iberian wild boar populations, where shelter influenced growth, productivity, and life expectancy. Though the wild boar is considered an omnivorous species, most of its diet (up to 90 %) consists of plants (Poland: Genov 1981a; Western Europe: Schley and Roper 2003). Our model indicated a positive influence of increasing proportions of deciduous and mixed forests on species abundance. In Poland, such forest habitats are dominated by heavy seed species: oak and/or beech. Every 3–8 years (mast years), these trees produce large amounts of seeds that constitute autumn–winter food for wild boars (Jędrzejewska et al. 1997). Jędrzejewska and Jędrzejewski (1998) documented a higher wild boar reproduction rate and better survival of piglets in the years following masting of oaks in the Białowieża Primeval Forest (Poland). Apart from seeds, deciduous forests supply wild boar with abundant food on the forest floor in the spring and summer (Faliński 1986) and high availability of edible starchy tubers and bulbs during winter (North Carolina and Tennessee, USA: Howe and Bratton

Fig. 5 Effects of environmental factors on wild boar abundance indices in Poland: results of generalized additive mixed models (GAMMs). The distribution of explanatory variable values is marked with *black vertical lines* on the x-axis. The y-axis presents the partial residuals of the model after removing the effects of the other covariates. The slope of zero indicates a constant influence of the covariates on wild boar abundance indices. *Dashed lines* correspond to 1 SE. Environmental factors: forest cover, January temperature, arable land, deciduous and mixed forest, marsh, and water



1976). Moreover, the soil of deciduous forests contains a large biomass of various forms of invertebrates (France: Baubet et al. 2003).

The positive influence of increasing proportion of marshes and water on wild boar abundance is generally explained by the same factors. Wild boars visit marshes and habitats connected with water bodies for feeding and wallowing (mud bathing) (France: Dardaillon 1987; Mediterranean wetlands: Vanschoenwinkel et al. 2008). Gimenez-Anaya et al. (2008) reported that up to 24 % of a wild boar's diet consisted of roots and bulbs of aquatic vegetation in a coastal Mediterranean wetland. High reeds and sedges serve as perfect shelter against unfavorable weather conditions, predators, and hunting pressure. The importance of habitats connected with water is highly seasonal and most important in summer when animals experience high temperatures and need a constant water supply for thermoregulation (Bracke 2011).

Past human pressures on deciduous and mixed forest (deforestation) resulted in a decreasing proportion of these forest habitats in Poland (presently approximately 25 % of the forest cover). This has resulted in a decline in the amount of optimal wild boar habitat and changed animal habitat utilization towards a more intensive use of arable land (Genov 1981b). Our model also confirmed the importance of arable land to wild boars. In Poland, crop plants (maize, wheat, potatoes) can constitute up to 81 % of their summer diet (Fruziński 1992). Interestingly, the proportion

of crops in a wild boar's diet drops substantially during mast years, resulting in lower damage levels on farmlands (Genov 1981a). Wild boar use farmlands mainly in the growing season (spring–autumn) but always prefer foraging close to shelters such as forest belts or high vegetation patches (Poland: Fonseca 2008; Japan: Honda 2009).

In wild boar populations, the major cause of density-independent mortality is severe winter conditions (Okarma et al. 1995; Melis et al. 2006). Deep snow and frozen soil constrain movements and foraging and disable rooting and the ability to obtain food (Melis et al. 2006). In addition, prolonged and unfavorable winter conditions (low temperature in early spring) directly influenced the survival of the newborn piglets in Switzerland (Geisser and Reyer 2005). Our data are concordant with previous reports on the negative impact of low winter temperatures on wild boars. The highest abundances of the species were found in western Poland where wild boar populations experience milder winter conditions than the eastern or southern (montane) populations.

We conclude that our findings may be applied in predicting future ungulate demographic and distribution trends in Poland, especially under ongoing changes directly connected with global warming and increasing forest cover. We expect that milder winter conditions will facilitate performance of these ungulates directly, which will result in the growth of their numbers. In addition, increasing temperatures will cause changes in ungulate habitats. In recent

decades, a shift in tree species composition has been observed in European forests with coniferous habitats being replaced by mixed and deciduous forests (Sykes et al. 1996). We presume that this process will increase ungulate food supply considerably and augment their populations. In Poland, all these changes will coincide with an increase in forest cover due to natural succession processes and the implementation of a national program of forest cover growth, which will presumably cause an additional increase in ungulate numbers.

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